A Mechanistic Model of Photosynthesis in Microalgae

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Abstract: A dynamic model of photosynthesis is developed, accounting for factors such as photoadaptation, photoinhibition, and the "flashing light effect." The model is shown to explain the reported photosynthesis–irradiance responses observed under various conditions (constant low light, constant intense irradiance, flashing light, diurnal variation in irradiance). As significant distinguishing features, the model assumes: (1) The stored photochemical energy is consumed in an enzyme-mediated process that obeys Michaelis-Menten kinetics; and (2) photoinhibition has a square-root dependence on irradiance. Earlier dynamic models of photosynthesis assumed a first-order dependence of photoinhibition on irradiance and different kinetics of consumption of the stored energy than used in this work. These earlier models could not explain the photosynthesis—irradiance behavior under the full range of irradiance scenarios—a shortcoming that is overcome in the model developed in this work. © 2003 Wiley Periodicals, Inc. *Biotechnol Bioeng* **81**: 459–473, 2003.

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INTRODUCTION

Photosynthesis is one of the very ancient biochemical processes that is the mainstay of almost all life on Earth. Of the total photosynthesis occurring on Earth, nearly half is associated with marine phytoplankton. Phytoplanktons cultured in photobioreactors are also useful for producing high-value biochemicals. Growth and production performance of a photosynthetic organism is obviously linked to the availability of light. The amount of light absorbed by an algal cell suspended in a photobioreactor depends on many factors, including the specific position of the cell at a given instance, the density of the culture, and the pigmentation of the cells. Predicting culture performance requires an understanding of the relationship between the growth observed and the amount of light received, or the photosynthesis–irradiance relationship (the *P-I* curve).

Many *P-I* relationships have been established empirically for specific cases (e.g., optically dilute culture, specific algae), as summarized elsewhere (Fasham and Platt, 1983; Goldman, 1979; Molina Grima et al., 1999; Zonneveld, 1998). Most of the available *P-I* models lack generality apparently because they were established purely empirically without considering the underlying biochemistry of photosynthesis. The kinetic constants of such empirical models are difficult to link to biological phenomena in the cell. Often, the empirical models fail to describe the well-known photoadaptive response of photosynthesis.

Photoadaptive processes can dramatically modify the growth–irradiance relationship (Zonneveld, 1998). One example of a photoadaptive response is the commonly observed increase in the concentration of the light-absorbing pigments in the cells exposed to low-intensity irradiance. Another important phenomenon that is generally disregarded in *P-I* models is photoinhibition, a decrease in the rate of photosynthesis that occurs when the irradiance level exceeds a certain value. Photoinhibition is well-documented (Denman and Marra, 1986; Harris and Lott, 1973; Marra, 1978) and it is associated with a partial deactivation of key components of the photosynthetic apparatus. To complicate matters, the various physiological responses to varying intensities of light can occur interactively. For example, the cells adapted to low-level irradiance are prone to greater photoinhibition when transferred to intense light.

In response to the many limitations of the fixed-parameter empirical *P-I* models (or 'static' models), more realistic 'dynamic' models of photosynthesis have been advanced (Eilers and Peeters, 1988; Fasham and Platt, 1983; Megard et al., 1984; Pahl-Wostl and Imboden, 1990; Zonneveld, 1998). The dynamic models typically breakdown the photosynthesis phenomenon into its individual steps, including at least one photochemical energy capture step

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and a metabolic consumption step. Differential equations are used to model these steps. Additional steps can be included to account for adaptive responses (Eilers and Peeters, 1988, 1993; Pahl-Wostl and Imboden, 1990; Zonneveld, 1998). Although the available dynamic models of photosynthesis do consider photoinhibition and photoadaptation, none of these models are sufficiently general. Existing models do not simultaneously account for photoadaptive responses (photoacclimation), photoinhibition, and the well-documented phenomenon known as the "flashing light effect" (Grobbelaar, 1994; Grobbelaar et al., 1996; Nedbal et al., 1996; Phillips and Myers, 1954; Terry, 1986). As demonstrated by the flashing light effect, continuous illumination of the microalgal culture is not necessary for supporting cell growth; growth can be quite efficiently promoted by intermittent or "flashing" light of the same intensity as the continuous light. The flashing light effect is of considerable significance in designing photobioreactors for algal culture. This is because the commercially viable culture systems must operate at high cell densities and, therefore, a photobioreactor necessarily contains an illuminated outer zone and a darker core. The movement of fluid between the illuminated zone and the dark interior unavoidably subjects the cells to fluctuating illumination.

In addition to lacking generality, the existing dynamic *P-I* models all assume a metabolic energy consumption rate that is either constant or proportional to the photochemical energy stored. As the main novelty, the present model is based on a metabolic control of the energy consumption through an enzyme-mediated process. (That is, regardless of the amount of energy harvested by the photosynthetic apparatus and stored as chemical energy, the rates of carbon dioxide fixation and biomass production are enzymatic processes that obey some rate law.) This implies that the maximum rate of energy consumption is not determined by the irradiance or the accumulated energy but by the nature of the microorganism. The metabolic energy consumption is an enzyme-mediated process and it is assumed to obey a Michaelis-Menten-type relationship, although any other relationship could have been used.

Also, the existing models typically interpret photoinhibition as a deactivation process that is assumed to obey first-order kinetics with respect to irradiance; however, this contradicts certain quantitative observations about photoinhibition occurring under intermittent light (Nedbal et al., 1996). Some of these problems are overcome in a general model of microalgal photosynthesis detailed in this article. The model combines the well-known biological concepts to account for the observed photoadaptation, photoinhibition, and culture growth (i.e., increase in cell mass or cell number) under intermittent light. The model is primarily intended for use in analysis of photobioreactors, but it is also useful for interpreting primary productivity (i.e., increase in cell mass per unit time per unit volume of fluid) of phytoplankton growth in natural waters.

MECHANISMS AND KINETICS

Photosynthesis

For modeling purposes, photosynthesis in a microalgal cell is assumed to occur only in the photosynthetic unit (PSU), a portion of the thylakoidal membrane that brings together photon receptors, electron carriers, and the enzymes necessary for generating NADPH and ATP (Prézelin, 1981; Zonneveld, 1998). Varying amounts of PSUs are harbored in chloroplasts. During photosynthesis, a resting-state or nonactivated PSU (A°) is first activated by absorption of photon. This initial light capture step is rapid and nonenzymatic. In subsequent steps, the activated PSU (A*) is slowly consumed in enzyme-mediated reactions that regenerate A°, provide energy for maintenance, and produce biomass. The fast and the slow steps of photosynthesis can be represented as Eq. (1) and Eq. (2), respectively:

$$\underbrace{\mathrm{A}^\circ}_{\text{resting PSU}} + \underbrace{h\nu}_{\text{photon}} \rightarrow \underbrace{\mathrm{A}^*}_{\text{activated PSU}} \text{ (fast photochemical reaction)} \tag{1}$$

$$\mathrm{A}^* \rightarrow \mathrm{A}^\circ \text{ (slow enzyme – controlled reaction).} \tag{2}$$

Although this second step involves the PSUs, its rate would be controlled by slower processes of the Calvin cycle.

At any instance, the total concentration of the photosynthetic units (a, mole PSU per cell) in the cell is of course the sum of the concentrations in the resting state (a^o) and in the activated state (a^*); i.e.,

$$a = a^\circ + a^* \tag{3}$$

Phytoplankton respond to the amount of light available by varying the size and concentration of the PSUs (Fasham and Platt, 1983; Prézelin, 1981); however, this process (photoacclimation) is much slower compared to the absorption of light and its assimilation by the cell. Thus, for the purpose of analyzing the kinetics of light absorption and metabolism, the concentration of PSUs can be assumed constant. The effects of photoacclimation are then reflected merely in changes in the values of the model parameters. Also, irradiance values above a certain intensity are known to reduce the amount of functional PSUs and this loss is manifested as photoinhibition. The photoinhibition and acclimation effects are considered in detail later in this article.

The light capture reaction [Eq. (1)] involves a direct interaction between a photon and the nonactivated PSU, A°. The rate r_1 of this reaction is expected to depend both on the concentration of the resting PSUs (a°) and the available irradiance I (mole photons $m^{-2} \cdot s^{-1}$); thus,

$$r_1 = k_a I \cdot a^\circ = k_a I(a - a^*) \tag{4}$$

where k_a is the absorption coefficient (m^2 per mole PSU). The product $k_a \cdot a^\circ$ (m^2 per cell) represents the effective absorption coefficient as a fraction of the total k_a.

Unlike the light capture reaction, the energy consumption reaction [Eq. (2)] is a multistep enzyme-mediated process.

Assuming a single controlling enzymatic step, the consumption rate, r_2, can be expressed as follows:

$$r_2 = \frac{r_m^* \cdot a^*}{K_S^* + a^*} \tag{5}$$

Thus, for a high concentration of activated PSUs (i.e., light-saturated growth), the consumption rate approaches a maximum, r_m^*, while the rate shows a linear dependence on a^* when the concentration of activated PSUs is similar to K_s (i.e., light-limited growth). Equation (5) is a Michaelis-Menten type relationship that is commonly observed for enzymatic reactions.

Because the light-capture reaction is so much faster than the subsequent enzyme-mediated reactions, the maximum rate of photosynthesis must be controlled by the concentration of one of the enzymes of the Calvin cycle (Sukenik et al., 1987). This rate is given by the quantity of enzyme catalyzing the step that gets saturated at the lowest concentration of activated PSUs. The value of r_m^* is the product of the limiting enzyme concentration and its rate constant and this can be expressed as the energy consumed per cell in unit time. This condition, also accepted by Zonneveld (1998), ensures that the rate of liberation of energy in the activated PSUs becomes a function of the amount of activated PSUs, which is consistent with an enzymatic control of the metabolic use of energy.

In Eq. (5), K_s represents the concentration of the activated PSUs that yields a photosynthesis rate equal to one-half of the maximum rate. As shown later, this equation can account for the enhanced yield in light use that is observed in experiments carried out under intermittent illumination, the flashing-light effect. The growth during the dark periods appears to be supported by the excess energy stored in the activated PSUs and that is slowly released by the enzymatic steps. In accordance with the assumptions described, the following balance equation can be written for the concentration of PSUs:

$$\frac{da^*}{dt} = k_a \cdot I \cdot (a - a^*) - \frac{r_m^* \cdot a^*}{K_S^* + a^*} \tag{6}$$

Photoinhibition

Photoinhibition is the net result of light-induced damage to photosystem II of the PSU, the repair mechanisms, and the photoprotective processes. The initial damage at photosystem II leads to inactivation of other systems, including the oxygen-evolving systems, the electron carriers, and the associated D1/D2 proteins. The cell repairs the damage over a course of hours.

The damage and recovery processes have vastly different rate constants: the radiation-induced photochemical damage is rapid but the biochemical regeneration of photosystem II is slow. However, compared to photosynthesis (time constant < 1 s), photoinhibition is a slow process with a time constant of the order of 1 h (Baroli and Melis 1996; Neidhardt et al., 1998; Samuelson et al., 1987). The polypeptide D1 is especially sensitive to excess light (Barber and Andersson, 1992). This protein has an average lifespan of 1 h under intense light and it is continuously synthesized in the chloroplast. Enhanced rates of protein synthesis have indeed been widely observed during photoinhibition (Samuelson et al., 1987). In the cyanobacterium *Synechococcus*, the synthesis of D1 protein during the photoinhibition repair process accounts for 10% of the total protein synthesis in the cell (Raven and Samuelson, 1986).

For modeling photoinhibition, a consideration of the experimental study conducted by Nedbal et al. (1996) is instructive. Nedbal et al. (1996) measured the changes in oxygen evolution caused by photoinhibition in three microalgae. The repair mechanisms in these studies were suppressed with streptomycin and only the deactivation mechanisms operated. Experiments with continuous and intermittent illumination at the same average irradiance values showed that for all three algae, photoinhibition was substantially stronger under continuous light and lower for intermittent illumination. The first-order deactivation rate constants for continuous illumination were approximately twice as high as the values for equivalent intermittent light.

These large differences in deactivation rates counter some of the assumptions made for modeling photosynthesis in earlier studies. For example, Megard et al. (1984) and Eilers and Peeters (1988, 1993) assumed that the rate of photodamage was proportional to the rate of photon absorption and the concentration of the activated PSUs. (Only photons in excess of those needed for PSU activation were assumed to damage the activated PSUs.) Similarly, Zonneveld (1998) assumed that the rate of damage was proportional to the rate of absorption of photons and the concentration of the functional D1 protein in the cells. In contrast to these assumptions, the results of Nedbal et al. (1996) suggest a reaction order of < 1 in photon absorption rate (or in instantaneous incident irradiance) for the photoinhibition process. (This is shown later on in this article.) Therefore, for modeling photoinhibition rate, we assume a reaction order of 0.5 in irradiance. In keeping with prior work, the photodamage rate is also assumed to depend on the total concentration (resting and activated) of functional PSUs. This is reasonable because functional D1 protein and other sensitive molecules occur both in resting and the activated PSUs. Thus, the photoinhibition rate is expressed as follows:

$$-\frac{d\,a_f}{d\,t} = k_i \sqrt{I}\, a_f \tag{7}$$

Here, a_f is the concentration of the functional PSUs (resting and activated) and k_i is a rate constant.

The 0.5 order of deactivation kinetics with respect I can be justified in view of the experiments reported by Nedbal et al. (1996) under different light regimes. For comparing photoinhibition in equivalent continuous light (I_c) and that under intermittent illumination ($I = I_c/\phi$), the mean root value of the irradiance $(\sqrt{I})_m$, in the two cases are related, as follows:

$$(\sqrt{I})_m = \frac{1}{t_c}\int_0^{t_c}\sqrt{I}\,dt = \nu\cdot\sqrt{\frac{I_c}{\phi}}\cdot\frac{\phi}{\nu} = \sqrt{\phi\cdot I_c} \qquad (8)$$

Here t_c is the characteristic time of the light–dark cycle, ν is the frequency, ϕ is the illuminated fraction of the cycle and I_c is the continuous irradiance. If Eq. (8) is used to compare continuous illumination to intermittent light (ν = 100 Hz, ϕ = 0.5) of the same mean irradiance I_c, we find that $(\sqrt{I})_m$ is smaller than $(\sqrt{I_c})_m$ by a factor of 1.414. Therefore, a 0.5 order in I agrees with the experimental results of deactivation kinetics obtained by Nedbal et al. (1996).

The assumption of $I^{0.5}$-dependence of the deactivation rate has the following rationale: if absorption of a photon deactivates a protective biomolecule D by breaking it into two radicals, i.e.,

$$D + h\nu \Leftrightarrow 2R^* \qquad (9)$$

and the process is reversible (the activated radicals can easily recombine to D), the concentration of the radicals will be proportional to the square root of the irradiance, because

$$K = \frac{[R^*]^2}{[D]\cdot I} \Rightarrow [R^*] = \sqrt{K\cdot[D]\cdot I} \propto \sqrt{I} \qquad (10)$$

The radicals $R^{\cdot}$ are very unstable and it is only in the presence of other substances (e.g., molecular oxygen), that the radicals may become stabilized by forming peroxides. The latter are sufficiently long-lived to attack and deactivate the various components of the PSU. This potentially accounts for the reported oxygen consumption during photoinhibition (Eilers and Peeters, 1993).

Published data (Nedbal et al., 1996) seem to indicate that, although photoinhibition is a slow process compared to the absorption and use of light, a change from continuous to intermittent illumination with a cycle time of 10 ms has a significant influence on the rate of this process. This suggests an instantaneous origin of the photoinhibiting process, such as a photochemical interaction represented in Eq. (9), and a later control exerted by a slower reaction. In any event, if the rate of photoinhibition can be expressed as Eq. (7) and the recovery process kinetics are first-order, then the following balance can be written for the concentration of the functional PSUs:

$$\frac{d\,a_f}{d\,t} = -\,k_i\sqrt{I}\,a_f + k_r\,a_{nf} = -\,k_i\sqrt{I}\,a_f + k_r\,(a_t - a_f) \qquad (11)$$

where k_r is the rate constant of the recovery process.

Under photoinhibition, the total concentration a of PSUs is replaced with the functional concentration, a_f, and the balance equation of activated centers now is:

$$\frac{da^*}{dt} = k_a\cdot I\cdot(a_f - a^*) - \frac{r_m^*\cdot a^*}{K_S^* + a^*} \qquad (12)$$

In summary, Eq. (11) and Eq. (12) represent the dynamics of photosynthesis and photoinhibition. The simplified mechanism of photosynthesis/photoinhibition assumed in this analysis is illustrated in Figure 1.

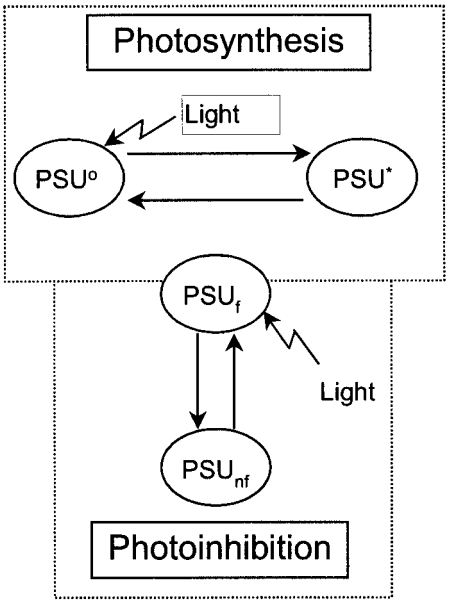

Figure 1. Schematic representation of photosynthesis and photoinhibition. A resting PSU (PSU^o) is activated to PSU* by absorption of light. Excess photons reversibly convert functional PSUs (PSU_f) to nonfunctional PSUs (i.e., PSU_{nf}).

SPECIFIC CASES OF THE MODEL

Here we detail the peculiar solutions of the model for two common cases: (1) Steady-state growth under constant continuous irradiance; and (2) growth under intermittent light. These cases span much of the data available on microalgal photosynthesis. Both the cases assume optically dilute cultures with little mutual shading. Many experimental studies satisfy this assumption, as discussed later in this article.

Continuous Illumination: The steady-state P-I Curve

For light-limited growth at steady-state under constant irradiance I, the balance of activated intermediates drawn from Eqs. (4) and (5) is:

$$0 = k_a\cdot I\cdot(a - a_e^*) - \frac{r_m^*\cdot a_e^*}{K_S^* + a_e^*} \qquad (13)$$

where a_e^* is a constant steady-state concentration of activated PSUs in the cell. By defining, $x_e^* = a_e^*/a$, as the steady-state fraction of the activated PSUs, Eq. (13) can be modified to the following:

$$(1 - x_e^*) = \frac{(\alpha/I)\cdot x_e^*}{\kappa + x_e^*} \qquad (14)$$

where

$$\frac{\alpha}{I} = \frac{r_m^*}{k_a\,a\,I};\ \kappa = \frac{K_S^*}{a};\ x_e^* = \frac{a_e^*}{a} \qquad (15)$$

A rearrangement of Eq. (14) yields the following quadratic equation:

$$(x_e^*)^2 - \left(1 - \kappa - \frac{\alpha}{I}\right) x_e^* - \kappa = 0 \tag{16}$$

which has the solution:

$$x_e^* = \frac{1}{2}\left[\left(1 - \kappa - \frac{\alpha}{I}\right) \pm \sqrt{\left(1 - \kappa - \frac{\alpha}{I}\right)^2 + 4\kappa}\right] \tag{17}$$

Only the positive of the two roots of Eq. (17) is physically meaningful. It is noteworthy that x_e^* must be always less than unity, regardless of the magnitude of the irradiance. This must be so because when x_e^* equals 1 (i.e., $a_e^* = a$) the absorption of energy ceases [Eq. (4)], implying a cessation of any measurable activity related to photosynthesis (e.g., oxygen generation, CO_2 fixation, growth, etc.). In view of this, any photosynthesis-related productivity measurement should be proportional to the metabolic rate of energy consumption; i.e.,

$$P = \frac{k_P r_m^* a^*}{K_S^* + a^*} = \frac{P_m x_e^*}{\kappa + x_e^*} \tag{18}$$

where

$$P_m = k_P r_m^* \tag{19}$$

and k_p is a proportionality constant.

Substituting Eq. (14) and the positive root of Eq. (17) in Eq. (18) gives the following:

$$\begin{aligned}\frac{P}{P_m} &= \frac{x_e^*}{\kappa + x_e^*} \\ &= \frac{I}{\alpha}(1 - x_e^*) \\ &= \frac{I}{2\alpha}\left[\left(1 - \kappa - \frac{\alpha}{I}\right) - \sqrt{\left(1 - \kappa - \frac{\alpha}{I}\right)^2 + 4\kappa}\right]\end{aligned} \tag{20}$$

Equation (20) provides the steady-state productivity of a light-limited culture growing under continuous illumination of a constant intensity, I, as a function of the parameters P_m, κ, and α defined above. The parameter P_m is a proportionality constant and its value depends on the specific response used to quantify the metabolic activity. The value of P_m only determines the maximum value of the *P-I* relationship and not its shape. The latter is controlled by the parameters κ and α.

The parameters P_m, κ, and α can be easily estimated from the experimental *P-I* data: P_m can be directly observed while α is readily derived from Eq. (20), as

$$\left(\frac{d(P/P_m)}{dI}\right)_0 = \frac{1}{\alpha}$$

A similar result was deduced by Fasham and Platt (1983). The parameter κ can be obtained from the limiting value of P/P_m, or

$$\lim_{I \to \infty} \frac{P}{P_m} = \frac{1}{1 + \kappa} \tag{21}$$

Equation (20) closely reproduces the generally observed trend of the *P-I* curve, including an initial zone of low-intensity illumination in which the fractional productivity (i.e., P/P_m) increases linearly with irradiance I, and a zone of higher illumination in which the rate of photosynthesis asymptotically approaches a maximum value. As examples, Figure 2 shows the fit of the present model [Eq. (20)] to the experimental data of Phillips and Myers (1954) and Terry (1986). These data were obtained with *Chlorella pyrenoidosa* (Phillips and Myers, 1954) and *Phaeodactylum tricornutum* (Terry, 1986). Both cultures were grown under continuous light and were optically thin.

The nondimensional group, α/I defined in Eq. (15) and which appears in Eq. (20) represents the ratio between the maximum rate of photosynthesis and the energy absorbed. When α/I is greater than unity, the light-absorption step controls the rate of the subsequent metabolic processes, as happens in the initial part of the *P-I* curve where the rate of photosynthesis depends strongly on irradiance. When α/I is less than unity, sufficient energy is available for the meta-

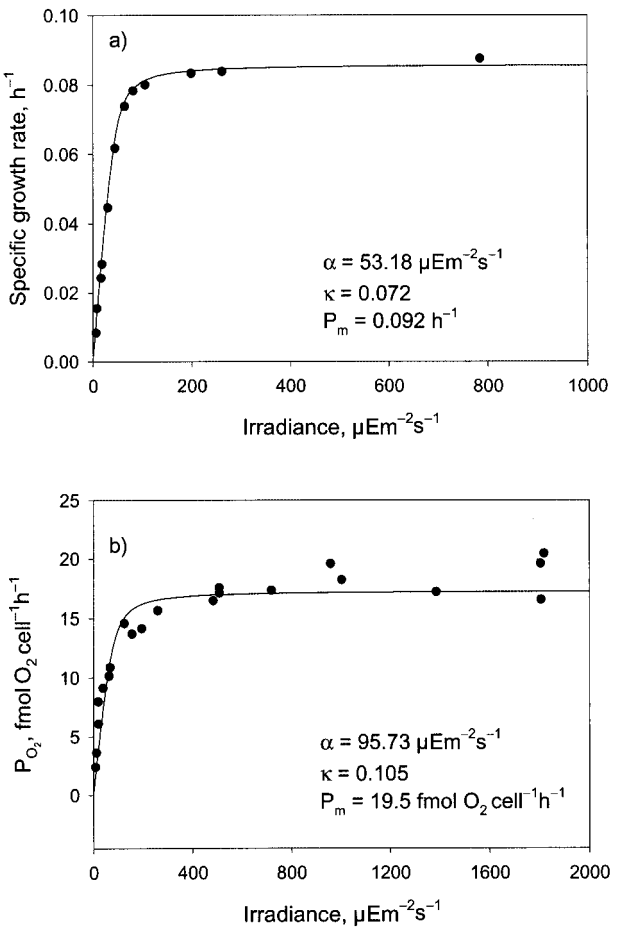

Figure 2. Fit of the model [Eq. (20)] to the data of: (a) Phillips and Myers (1954); and (b) Terry (1986). The best fit values of α, κ, and P_m are noted for each case.

bolic processes to become saturated and the rate of photosynthesis is no longer a strong function of the irradiance (i.e., metabolic assimilation of energy becomes the rate-controling step). Increasing values of α (same units as *I*) cause the point of transition between the initial and the flat parts of the *P-I* curve to displace to higher values of irradiance, as shown in Figure 3a. Thus, when *I* happens to equal α, Eq. (20) becomes

$$\frac{P}{P_m} = \frac{1}{2}\left[\left(2+\kappa\right) - \sqrt{\kappa^2 + 4\kappa}\right] \tag{22}$$

For the κ value used in Figure 3a, α is the irradiance that provides a fractional productivity (P/P_m) value of 0.8. The parameter κ represents the fraction of the activated PSUs that give rise to a fractional productivity of 0.5. Increasing the value of κ decreases the observed maximum of the *P-I* curve, as shown in Figure 3b.

Because $0 < x_e^* < 1$, the observed productivity will be always less than the true maximum given by Eq. (19), except for very low values of κ. As shown in Figure 2a, for *C. pyrenoidosa* κ is 7.2% of the functional PSUs. As discussed later, κ is also influenced by the light exposure history of the cell. As Eq. (20) implies, if Figure 3a is redrawn by plotting the values of P/P_m vs. I/α (instead of *I*), the four curves shown would collapse into a unique plot with a P/P_m value at $I/\alpha = 1$ as given by Eq. (22). Furthermore, for high values of I/α, the P/P_m value would approach $(1/1 + \kappa)$, as expected from Eq. (21).

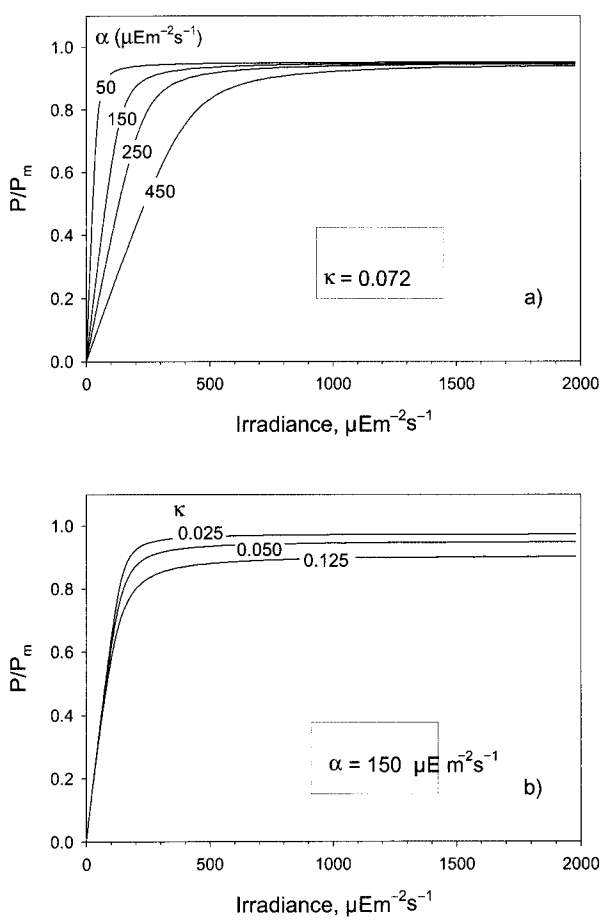

Figure 3. Fractional rate of photosynthesis vs. irradiance: (a) influence of the parameter α; and (b) influence of the parameter κ.

Photoinhibition Under Steady-State Continuous Illumination

When the culture is photoinhibited at steady-state, Eq. (11) leads to the expression:

$$a_f = \frac{a_t}{1 + \delta\sqrt{I}} \tag{23}$$

where

$$\delta = \frac{k_i}{k_r} \tag{24}$$

To include the effect of photoinhibition in the various equations of the model described in the preceding parts, we only need to substitute *a* with a_f. This accounts for a certain fraction of the total PSU population becoming nonfunctional.

Correcting for photoinhibition requires two steps. First, all the system parameters need to be modified because they all contain implicitly the concentration of the functional PSUs. Thus, using the definitions in Eq. (15), we have:

$$\kappa = \frac{K_S^*}{a_f} = \frac{K_S^*}{a_t}\left(1 + \delta\sqrt{I}\right) = \kappa_t\left(1 + \delta\sqrt{I}\right) \tag{25}$$

$$\alpha = \frac{r_m^*}{k_a a_f} = \frac{r_m^*}{k_a a_t}\left(1 + \delta\sqrt{I}\right) = \alpha_t\left(1 + \delta\sqrt{I}\right) \tag{26}$$

where the subscript *t* denotes that the parameters are now referred to the total amount of PSUs, both functional and nonfunctional. Using Eqs. (25)–(28), the model can be expressed in terms of the total concentration of PSUs. This is a convenient transformation because, despite photoadaptation, the total PSU concentration is relatively constant in the medium term compared to the concentration of the functional PSUs. Also, the total concentration of PSUs is easier to measure than the concentration of functional PSUs.

Secondly, the calculation of the fractional productivity [Eq. (20)] should be corrected to account for photoinhibition; thus,

$$\left(\frac{P}{P_m}\right)_i = \frac{I}{\alpha}\left(1 - x_e^*\right) = \frac{K_d I}{r_m^*} a_f \left(1 - x_e^*\right) \tag{27}$$

In Eq. (27), a_f should be replaced with a_t when no photoinhibition occurs.

Comparing these two cases [i.e., Eq. (27) for the cases of photoinhibition and no photoinhibition], it is obvious that

$$\begin{aligned}\left(\frac{P}{P_m}\right)_i &= \left(\frac{P}{P_m}\right)\cdot\frac{a_f}{a_t} \\ &= \left(\frac{P}{P_m}\right)\cdot\left(\frac{1}{1+\delta\sqrt{I}}\right) \\ &= \frac{I}{\alpha}\left(1 - x_e^*\right)\left(\frac{1}{1+\delta\sqrt{I}}\right)\end{aligned} \tag{28}$$

Equation (28) should be used [instead of Eq. (20)] for photoinhibited culture. Equation (28) takes into account the fact that some of the PSUs in photoinhibited culture are nonfunctional.

Figure 4a and 4b shows the modeled P/P_m vs. irradiance curves produced with Eq. (28). The plots are for continuous illumination, accounting for photoinhibition, and for two different values of α_t. From Figure 4, the fractional productivity attains a maximum that decreases when the parameter δ is increased. The shape of the curves shown suggests that the model can be used to fit the type of data presented in Figure 2a and 2d of Fasham and Platt (1983); however, the curves (Fig. 4) do not seem satisfactory for explaining the type of data given in Figure 2b and 2c of the same article. In the latter cases, the productivity attained a broad plateau and then declined sharply with further increase in irradiance. This suggests that at high irradiance values, other mechanisms of photoinhibition may operate in parallel with the one discussed.

Intermittent Illumination

For intermittent illumination (light/dark cycling) in optically thin cultures without photoinhibition, Eq. (12) holds for the light period. Equation (12) also holds during the dark period but with a null light absorption, that is,

$$\frac{d\,a^*}{d\,t} = -\frac{r_m^*\,a^*}{K_S^* + a^*} \tag{29}$$

For applying Eq. (12) and Eq. (29) to intermittent illumination, we define a dimensionless time ϕ as follows:

$$\phi = \frac{t_f}{t_c} \tag{30}$$

where t_c is the duration of the light cycle, i.e.,

$$t_c = t_f + t_d = \frac{1}{\nu} \tag{31}$$

where t_f is the duration of illumination and t_d is the length of the dark period within one light/dark cycle and ν is the frequency of the cycle. Using the definitions given by Eq. (30) and Eq. (31), and replacing a^* with the fraction of activated PSUs (i.e., x^*), Eq. (12) and Eq. (29) can be transformed to Eq. (32) and Eq. (35), respectively:

$$\frac{d\,x^*}{d\,\tau} = \frac{k_a\,I}{\nu}\left((1-x^*) - \frac{(\alpha/I)\,x^*}{\kappa + x^*}\right) \tag{32}$$

$$\tau = 0 \rightarrow x^* = x^*_{min} \tag{33}$$

$$\tau = \phi \rightarrow x^* = x^*_{max} \tag{34}$$

$$\frac{d\,x^*}{d\,\tau} = -\frac{k_a\,\alpha}{\nu}\left(\frac{x^*}{\kappa + x^*}\right) \tag{35}$$

$$\tau = \phi \rightarrow x^* = x^*_{max} \tag{36}$$

$$\tau = 1 \rightarrow x^* = x^*_{min} \tag{37}$$

Equations (32)–34) are for the light period of the cycle while Eqs. (35)–(37) apply to the dark period. The limits given in Eqs. (33), (34), (36), and (37) are necessary to ensure that the value of x^* (i.e., the fraction of activated PSUs) is the same at the transition from light to dark and vice-versa, once a steady-state has been reached.

The coefficients on the right-hand sides of Eqs. (32) and (35) can be expressed as follows:

$$\frac{k_a\alpha}{\nu} = \frac{r_m^*}{a\,\nu} = \frac{\beta}{\nu};\quad \frac{k_a I}{\nu} = \frac{k_a\,\alpha}{\nu}\frac{I}{\alpha} = \frac{\beta}{\nu}\frac{I}{\alpha} \tag{38}$$

where

$$\beta = \frac{r_m^*}{a} \tag{39}$$

The parameter β is a characteristic frequency of the system and it represents the maximum specific rate of photosynthesis.

Separating the variables in Eq. (32), we obtain:

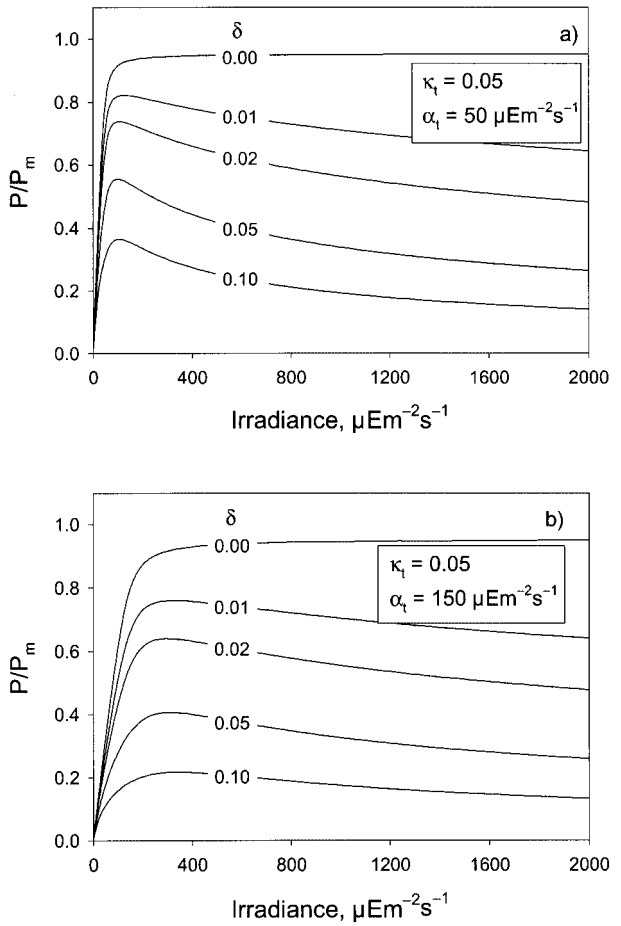

Figure 4. Fractional rate of photosynthesis versus irradiance: Effect of the photoinhibition parameters α_t and δ.

$$\int_{x^*_{min}}^{x^*} \frac{\kappa + x^*}{(x^* - x_1^*)(x^* - x_2^*)} = \frac{\beta I}{\nu \alpha} \tau \tag{40}$$

where x_1^* and x_2^* are the two roots of Eq. (17). Integrating from the start of the light period to any given time within it, we have:

$$\frac{\kappa + x_1^*}{x_1^* - x_2^*} \ln\left(\frac{x^* - x_1^*}{x^*_{min} - x_1^*}\right) - \frac{\kappa + x_2^*}{x_1^* - x_2^*} \ln\left(\frac{x^* - x_2^*}{x^*_{min} - x_2^*}\right) = \frac{\beta I}{\nu\alpha} \tau \tag{41}$$

Equation (41) can be rearranged to the following:

$$\frac{1}{x_1^* - x_2^*} \ln\left(\left(\frac{x^* - x_1^*}{x^*_{min} - x_1^*}\right)^{\kappa + x_1^*} \left(\frac{x^*_{min} - x_2^*}{x^* - x_2^*}\right)^{\kappa + x_2^*}\right) = \frac{\beta I}{\nu \alpha} \tau \tag{42}$$

Similarly, the integration of Eq. (35) from the beginning of the dark to any time within it, leads to:

$$\kappa \ln\left(\frac{x^*_{max}}{x^*}\right) + x^*_{max} - x^* = \frac{\beta}{\nu}(\tau - \phi). \tag{43}$$

In Eq. (42) and Eq. (43), x_m^* and x_m^* are found by solving these equations, respectively, for the whole duration of light ($\tau = \phi$) and dark ($\tau = 1 - \phi$); thus,

$$\frac{1}{x_1^* - x_2^*} \ln\left(\left(\frac{x^*_{max} - x_1^*}{x^*_{min} - x_1^*}\right)^{\kappa + x_1^*} \left(\frac{x^*_{min} - x_2^*}{x^*_{max} - x_2^*}\right)^{\kappa + x_2^*}\right) = \frac{\beta}{\nu} \frac{I}{\alpha} \phi \tag{44}$$

$$\kappa \ln\left(\frac{x^*_{max}}{x^*_{min}}\right) + x^*_{max} - x^*_{min} = \frac{\beta}{\nu}(1 - \phi) \tag{45}$$

This system of two nonlinear equations can be solved numerically for any selected values of the characteristic parameters of the system (i.e., α, κ, and β) and the known operational variables of the light-dark cycle (i.e., I, ϕ and ν). Note that the characteristic parameters α and β have the same dimensions as I and ν, respectively. Consequently, the kinetics of photosynthesis can be described by the following four dimensionless parameters: κ, α/I, β/ν, and ϕ.

As in continuous light, the fractional mean productivity under intermittent illumination will be proportional to the metabolic rate of energy consumption in both the light and the dark periods of the cycle. Thus, for intermittent light, the equivalent of Eq. (18) is the following:

$$\frac{\overline{P}}{P_m} = \int_0^1 \frac{x^*}{\kappa + x^*} d\tau \tag{46}$$

Equation (46) needs to be solved with either Eq. (42) or Eq. (43), to obtain a relationship between x^* and t in the light and dark periods, respectively.

Considering Eq. (32), during the light period the following relationship applies:

$$\frac{x^*}{\kappa + x^*} = \frac{I}{\alpha}(1 - x^*) - \frac{\nu}{\beta} \frac{d\,x^*}{d\,\tau} \tag{47}$$

and the integration of its leftmost part during the light period gives

$$\int_0^\phi \frac{x^*}{\kappa + x^*} d\tau = \frac{I}{\alpha} \int_0^\phi (1 - x^*)\, d\tau - \frac{\nu}{\beta}(x^*_{max} - x^*_{min}) \tag{48}$$

Similarly, Eq. (35) implies that during the dark period the following applies:

$$\frac{x^*}{\kappa + x^*} = \frac{\nu}{\beta} \frac{d\,x^*}{d\,\tau} \tag{49}$$

that can be integrated for the dark period to obtain:

$$\int_\phi^1 \frac{x^*}{\kappa + x^*} d\tau = \frac{\nu}{\beta}(x^*_{max} - x^*_{min}) \tag{50}$$

Equation (46), which applies to the entire light-dark cycle, can be therefore obtained by summing Eq. (48) and Eq. (50); thus,

$$\int_0^1 \frac{x^*}{\kappa + x^*} d\tau = \frac{I}{\alpha} \cdot \int_0^\phi (1 - x^*) \cdot d\tau \tag{51}$$

and therefore

$$\frac{\overline{P}}{P_m} = \frac{I}{\alpha} \int_0^\phi (1 - x^*) \cdot d\tau \tag{52}$$

Equation (52) suggests that the energy driving photosynthesis is only harvested by resting PSUs (i.e., $1 - x^*$) during the illuminated periods. However, this does not negate the possibility of photosynthetic production occurring during the dark periods, as proposed by Eilers and Peeters (1993), because a part of the energy harvested during the light period and which remains stored in the activated PSUs can support the metabolic demand. As long as the dark period is not too lengthy, or the cycle frequency is high enough for the activated fraction of PSUs to remain greater than κ during the entire cycle, the fractional productivity in cycling conditions will be similar to that obtained under continuous illumination.

Another parameter that is sometimes used to discuss photosynthesis under intermittent light is the light "integration function" (Γ) defined by Terry (1986), as follows:

$$\Gamma = \frac{\overline{P} - \phi\, P(I)}{P(I_m) - \phi\, P(I)} \tag{53}$$

Under full integration of light, the Γ value is 1 and in this case the mean fractional productivity can be calculated with Eq. (20) using the mean irradiance defined as follows:

$$I_m = \frac{t_f}{t_f + t_d} I = \phi\, I \tag{54}$$

Note that Γ is independent of P_m because all three specific productivities in Eq. (53) are proportional to P_m and this eliminates P_m.

In summary, the behavior of an optically thin culture growing under intermittent illumination can be described by four dimensionless parameters—κ, α/I, β/ν and ϕ; however, it is better to consider independently the values of κ,

Table I. Influence of the operating variables (I, ϕ, ν) on the predicted performance (P/P_m, Γ).

Operational parameters			Results		
I (E · m^{-2}s^{-1}	ϕ	ν(s^{-1})	P/P_m	Γ	ε
1000	0.25	1.0	0.641	0.608	0.385
1000	0.25	0.5	0.446	0.316	0.268
1000	0.25	2.0	0.861	0.939	0.516
1000	0.50	1.0	0.876	0.872	0.263
1000	0.75	1.0	0.935	0.969	0.187
2000	0.25	1.0	0.694	0.655	0.208

Note: Model parameters: $\kappa = 0.05$, $\alpha = 150$ E · m^{-2}s^{-1}, $\beta = 2$ s^{-1}.

α, and β (the system or organism parameters) to clearly see the influence of the operating variables I, ν, and ϕ.

The computed variation in the fraction of activated PSUs is shown in Figure 5 as function of the dimensionless time in a full light-dark cycle. The results are shown for two cycle frequencies. The vertical line in Figure 5 marks the boundary between the light and the dark periods; the horizontal lines indicate the calculated fraction of the activated PSUs for the cases of continuous illumination at a constant irradiance (I) and the time averaged irradiance ($\phi \cdot$ I) of an equivalent continuous illumination. The plot for unit frequency ($\nu = 1$ s^{-1}) shows that the fraction x_e^* of the activated PSUs initially increases sharply but the rate of increase slows down when x_e^* approaches the steady-state value for the irradiance level used in the simulation. In contrast, the decay rate of the PSU fraction during the dark period is approximately constant until the x_e^* value has approached κ. The x_e^* value declines to zero during a substantial part of the dark period and this reduces both the mean fractional productivity and the integration function Γ. If the cycle frequency is increased to 2 s^{-1}, and the other variables are kept unchanged, the x_e^* value never reaches zero and the mean productivity (and the integration function Γ) is greater than was the case with $\nu = 1$ s^{-1}.

The influence of the operating variables (I, ϕ, ν) on the model-predicted performance indices (i.e., P/P_m, Γ) is shown in Table I. The table also records the ratio ε, defined as follows:

$$\varepsilon = \frac{\overline{P}/P_m}{\phi\, I/\alpha} = \frac{\overline{P}/P_m}{I_m/\alpha} \tag{55}$$

ε is the ratio between the attained fractional productivity and the mean irradiance on the cells, expressed as units of α. ε may be thought of as a measure of the photosynthetic efficiency. The model-predicted photosynthetic efficiency ε

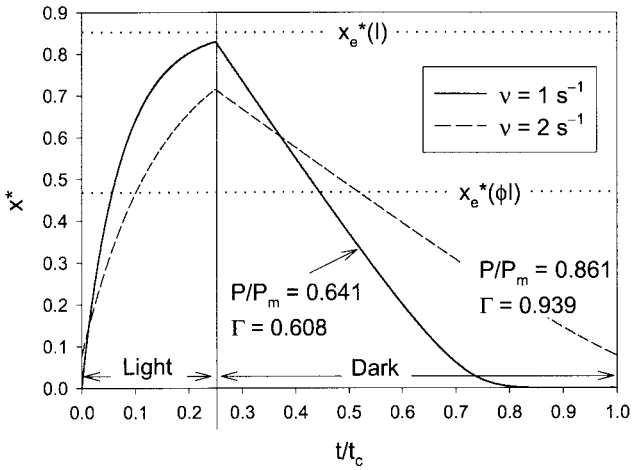

Figure 5. Activated fraction x_e^* of PSUs vs. the dimensionless time t/t_c of the light-dark cycle for two values of the cycle frequency ν.

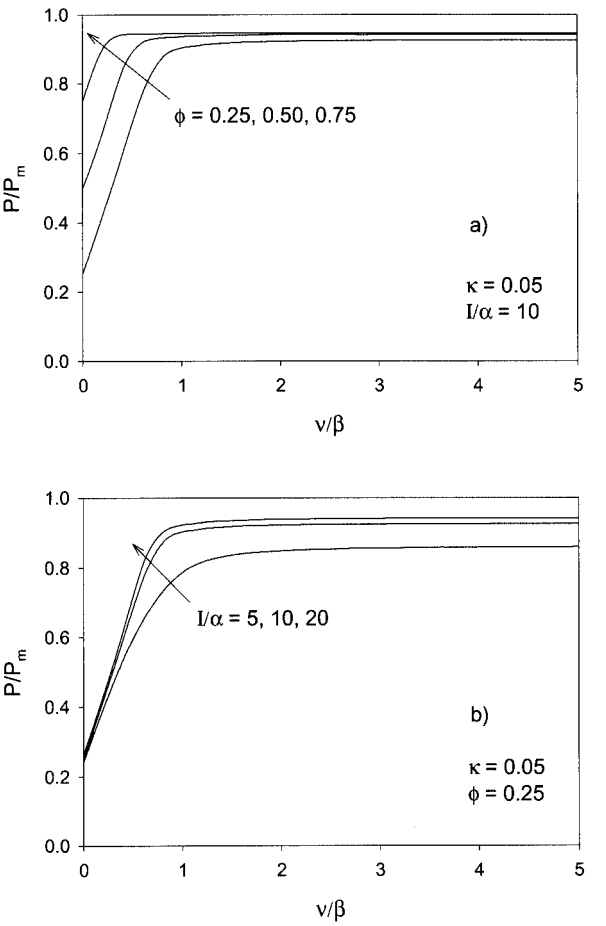

Figure 6. Fractional productivity P/P_m vs. the dimensionless frequency ν/β: (a) effect of the illuminated fraction ϕ of the cycle; (b) effect of the dimensionless irradiance I/α.

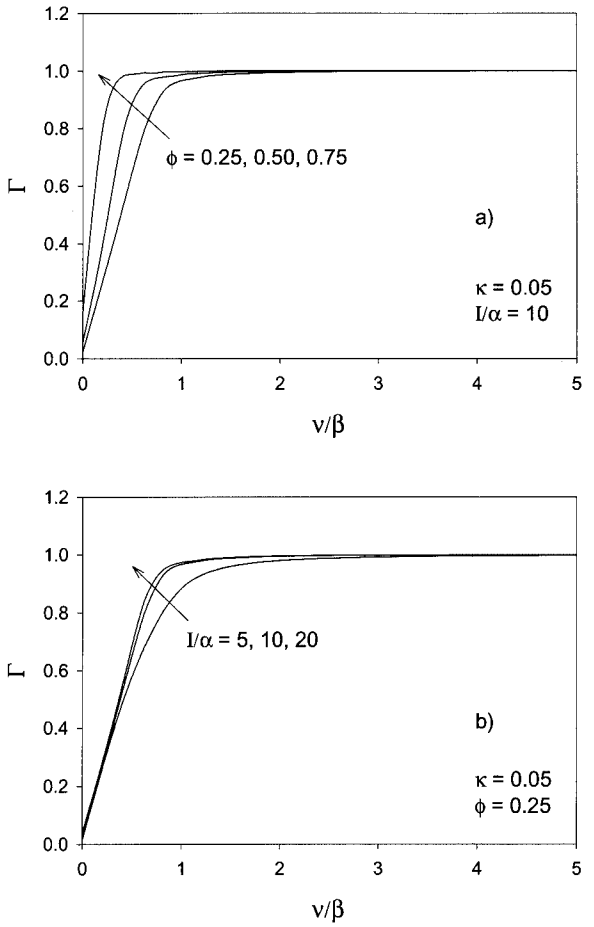

Figure 7. The integration function Γ vs. the dimensionless frequency ν/β: (a) effect of the illuminated fraction ϕ of the cycle; (b) effect of the dimensionless irradiance I/α.

is increased by using light of a higher frequency (Table I); however, an extension of the illuminated fraction of the light-dark cycle causes an increased fractional productivity and the light integration function, but a decrease in the photosynthetic efficiency (Table I). It is also shown that when the incident irradiance is increased, the fractional productivity and the integration function show only a slight increase while the photosynthetic efficiency is substantially decreased.

Figure 6 shows the predicted fractional productivity as a function the dimensionless frequency, ν/β, for different values of the illuminated fraction, ϕ (Fig. 6a), and also for different values of the dimensionless irradiance, I/α (Fig. 6b). In both cases, when $\nu/\beta > 1$, the fractional productivity is close to its maximum value and is little affected by other parameters. Obviously, when the illuminated fraction increases, the fractional productivity increases at $\nu/\beta = 0$ (Fig. 6a). The rate of increase of $P(I)/P_m$ depends on the dimensionless irradiance (I/α) which is constant at 10 for the plots in Figure 6a. The maximum value attained for the productivity is obtained by multiplying the productivity at given irradiance with the illuminated fraction of the cycle; therefore, the maximum fractional productivity is $P(\phi I)/P_m$. The situation in Figure 6b is different: the fractional productivity increases at different rates from a common origin. The rate of increase depends on the value of $I/\alpha$and reaches different maximum values.

For the same variables as in Figure 6, the integration function Γ is plotted in Figure 7 as a function of the dimensionless frequency ν/β. Not surprisingly, the integration function is quite close to unity for $\nu/\beta > 1$ and is little affected by the illuminated fraction ϕ and the nondimensional irradiance I/α. The model-predicted plots in Figures 6 and 7 are identical to those derived from experimental data and given in Figures 4–6 of Terry (1986).

Figure 8 shows the influence of ϕ on the fractional productivity, at different values of the nondimensional frequency ν/β. The line topping of the family of plots corresponds to a continuous illumination equivalent to the intermittent light of the other plots. Obviously, the plot for $\nu/\beta = 1$ is quite close that for continuous illumination. The plots move away from the continuous light curve and straighten, as ν/β declines. The shape of these curves is quite similar to the experimental data presented in Figure 1 of Kok (1953) and Figure 3 of Nedbal et al. (1996).

The influence of the mean dimensionless irradiance ($\phi I/\alpha$) on the fractional productivity is shown Figure 9 for different values of the dimensionless frequency ν/β. The line for equivalent continuous irradiance is also shown. As in Figure 8, the plot corresponding to $\nu/\beta = 1$ comes close to that of the equivalent continuous light. The maximum attainable P/P_m value declines as ν/β decreases.

Finally, Figure 10 shows the variation of the relative photosynthesis rate with changes in the duration of the light period, while keeping constant the ratio between the light and dark times. This figure allows a comparison of the model with some published data that has been presented in this way. The plots in Figure 10 agree with the ones in Figure 2 of Kok (1953) and those in Figure 2 of Nedbal et al. (1996). In summary, Figures 7, 8, and 10 confirm that the model developed in this work explains at least qualitatively

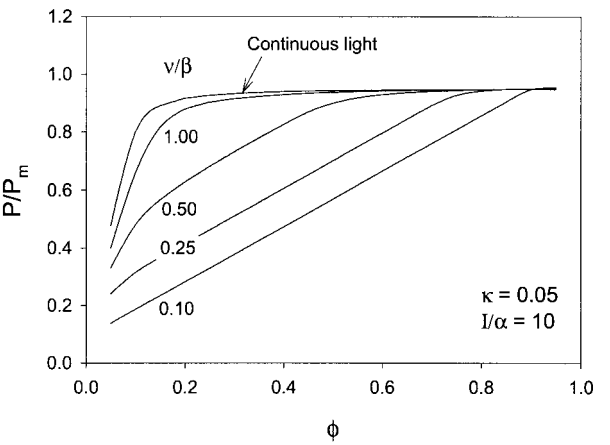

Figure 8. Fractional productivity P/P_m vs. the illuminated fraction ϕ for various values of the dimensionless frequency ν/β.

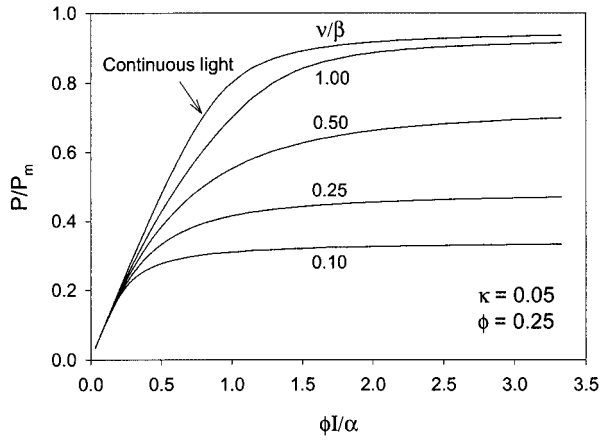

Figure 9. Fractional productivity P/P_m versus $\phi \cdot I/\alpha$ for various values of the dimensionless frequency ν/β.

many of the responses observed for photosynthesis in dilute cultures under intermittent illumination.

Photoinhibition in intermittent light

For photoinhibition under intermittent illumination of a certain frequency, the concentration of functional PSUs is calculated with Eq. (23). Also, if Eq. (8) is used to compare photoinhibition under intermittent illumination and its equivalent continuous illumination, it can be shown that:

$$(\sqrt{I})_m = \sqrt{\phi \cdot I_c} \Rightarrow \sqrt{I_c} \geq (\sqrt{I})_m \qquad (56)$$

where ϕ is the illuminated fraction of the light-dark cycle ($\phi = 1$ for continuous light and $\phi < 1$ for other cases). Thus, the magnitude of photoinhibition under continuous light is always greater than under intermittent light. This explains the observation that intermittent light can provide a higher productivity than the equivalent continuous illumination (Grobbelaar, 1994; Grobbelaar et al., 1996; Nedbal et al., 1996; Philliphs and Myers, 1954; Terry, 1986).

The fractional productivity under photoinhibition is obtained by using the following equation:

$$\left(\frac{\overline{P}}{P_m}\right)_i = \frac{\overline{P}}{P_m}\left(\frac{1}{1+\delta(\sqrt{I})_m}\right) = \left(\frac{1}{1+\delta\,\phi\,\sqrt{I}}\right)\frac{I}{\alpha}\int_0^{\phi}(1-x^*)\,d\tau \qquad (57)$$

Equation (57) is obtained from Eq. (52) and Eq. (28).

The fractional productivity calculated with Eq. (57) and the corresponding Γ-values are shown in Figures 12 and 11, respectively. These figures are the equivalents of Figure 7b and Figure 8, respectively, but they now include the effect of photoinhibition. According to Figure 11, the integration function exceeds unity for high-cycle frequencies. This is because photoinhibition is more intensive under continuous light than under intermittent illumination. This effect is seen again in Figure 12 where the fractional productivity under intermittent light becomes greater than fractional productivity under continuous light when ν/β is unity. Comparing Figures 8 and 12, however, it is obvious that photoinhibition decreases the fractional productivity compared to uninhibited culture.

Application to Published Data

Here, the proposed model is used to explain some published data obtained for growth in flashing light (Nedbal et al., 1996; Philliph and Myers, 1954). The available data are also used to obtain the best-fit values of the model parameters, α, β, κ, and P_m. The parameters were obtained by nonlinear regression that minimized the difference between the model predictions and the experimental observations.

The best-fit parameter values were $P_m = 0.12\ h^{-1}$, $\alpha = 22724\ erg \cdot cm^{-2}s^{-1}$ (91.0 $\mu E \cdot m^{-2}s^{-1}$), $\kappa = 0.27$ and $\beta = 15.22\ s^{-1}$ for the 17 experiments of Philliph and Myers (1954). The best-fit model parameter values obtained for the data of Nedbal et al. (1996) were: $P_m = 89.23\ \mu mol\ O_2$ per

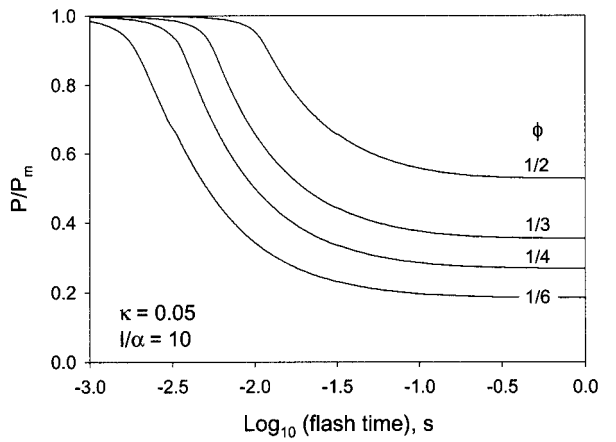

Figure 10. Fractional productivity P/P_m vs. the duration of the flash period for various values of the illuminated fraction ϕ of the light-dark cycle.

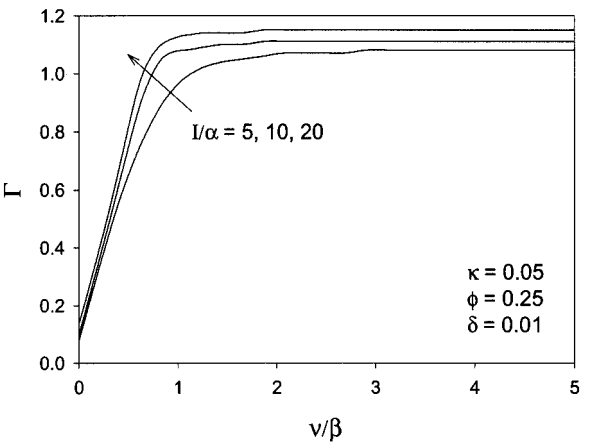

Figure 11. Integration function Γ versus the dimensionless frequency ν/β for various values of the dimensionless irradiance I/α in photoinhibited culture.

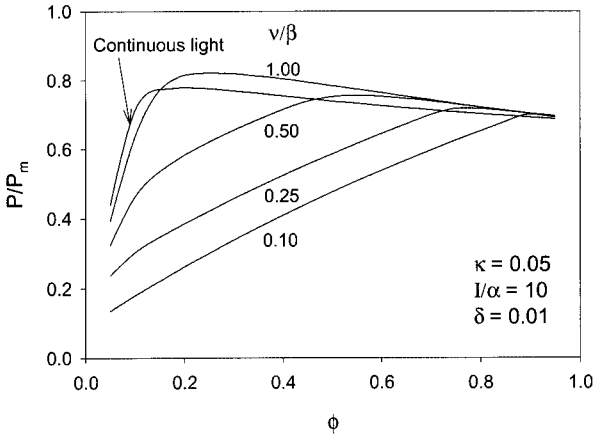

Figure 12. Fractional productivity P/P_m vs. the illuminated fraction ϕ for various values of the dimensionless frequency ν/β in photoinhibited culture.

mmol chlorophyll $\cdot$ s^{-1}, $\alpha = 899$ $\mu E \cdot m^{-2}s^{-1}$, $\kappa = 0.14$, and $\beta = 70.40$ s^{-1}. For the purposes of this analysis, the graphically presented data of Nedbal et al. (1996) was first digitized. The measured values of the specific growth rate compared closely with the model-derived values, as shown in Figure 13 for the two sets of data. In both cases, a vast majority of data agreed with the model within ± 20%. Clearly, the model is capable of a good quantitative fit to data obtained under flashing light and can be reasonably expected to correctly estimate photosynthetic responses under other variable-light regimes.

Photoacclimation

Cells are known to adapt the number and size of PSUs to the available irradiance when irradiance is constant for a prolonged period (Fasham and Platt, 1983; Prézelin, 1981). Cells acclimated to high irradiance have fewer PSUs and these contain less chlorophyll than the same cells growing under low irradiance. This acclimation response is slower than photoinhibition (Berner et al., 1989).

It seems reasonable that through photoacclimation the cells will adapt to acquire the necessary number and size of PSUs to capture all the energy that a cell is capable of metabolizing, thus maintaining a situation of enzymatic control of the metabolism. Under high irradiance, the enzymatic control occurs when:

$$k_a I a_f = r_m^* \tag{58}$$

and a cell needs to have the following amount of functional PSUs:

$$a_f = r_m^*/k_a I \tag{59}$$

In addition, if there is photoinhibition, the total amount of PSUs should be:

$$a_t = \left(\frac{r_m^*}{k_a I}\right)(1 + \delta\sqrt{I}) \tag{60}$$

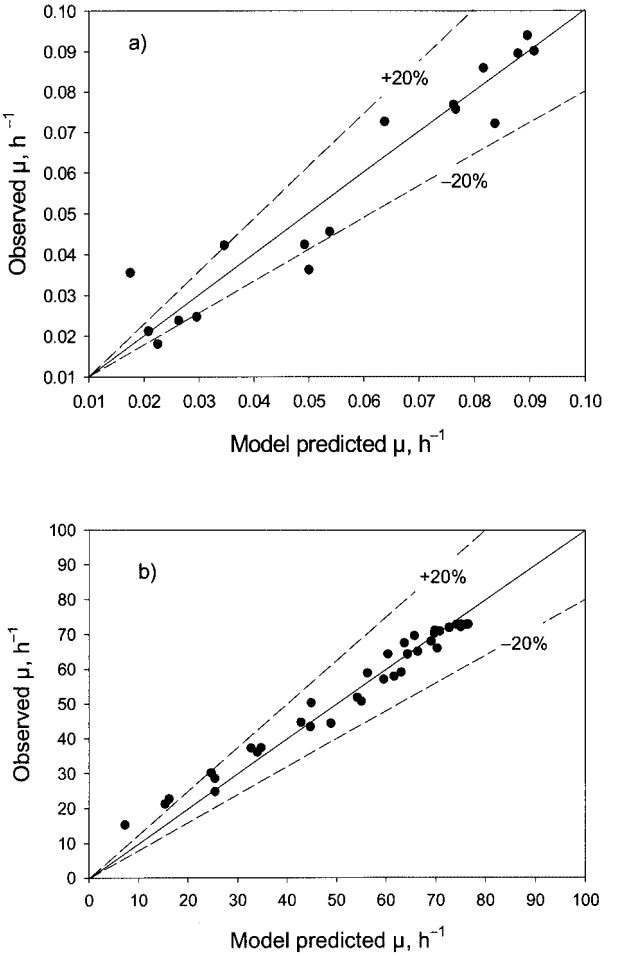

Figure 13. Observed specific growth rate vs. model-predicted specific growth rate: (a) data of Philliph and Myers (1954); and (b) data of Nedbal et al. (1996). The solid lines indicate exact agreement.

Therefore, the total PSU concentration under high irradiance is expected to be:

$$a_t = \frac{r_m^* \delta}{k_a \sqrt{I}} \tag{61}$$

In contrast, under low irradiance, the concentration of PSUs in the cell increases (Berner et al., 1989) and the resulting mutual shading among PSUs poses a limitation on the photosynthetic performance (Zonneveld, 1998). There is an upper limit on the rate of absorption, established by the cross section of the cell that is normal to light, and this determines a maximum value for a_t; thus,

$$(a_t)_{max} = \frac{r_m^*}{k_c} \tag{62}$$

where k_c is a rate constant. Equations (61) and (62) for the two mentioned limits can be integrated into a single hyperbolic function, as proposed by Zonneveld (1998):

$$a_t = \frac{r_m^*}{k_c + \dfrac{k_a\sqrt{I}}{\delta}} \tag{63}$$

Equation (63) was used to interpret the results obtained by Sukenik et al. (1987) with *Dunaliela tertiolecta* growing under different irradiances. Sukenik et al. (1987) measured the cellular concentrations of the various biochemical components of the PSUs (Photosystems I and II, cytochrome b_6f, Rubisco enzyme) in cells grown at irradiance values between 80 and 1900 $\mu E \cdot m^{-2}s^{-1}$. The concentrations of the components of the PSUs were found to decrease continuously when the irradiance was increased; however, the cellular concentration of the Rubisco enzyme (apparently the rate controling enzyme of the Calvin cycle) remained constant. Equation (63), rearranged to,

$$\frac{1}{a_t} = \frac{k_c}{r_m^*} + \frac{k_a \sqrt{I}}{\delta\, r_m^*} \tag{64}$$

could be used fit the results obtained by Sukenik et al. (1987) (Fig. 14), suggesting that the model is potentially capable of accommodating photoacclimation effects.

Photoinhibition in Continuously Varying Irradiance

Here we discuss the behavior of the model under conditions of continuously varying irradiance, for example, during typical outdoor culture. For this purpose, the system of coupled differential Eqs. (11) and (12), which completely describes the dynamics of the model, was rearranged by dividing by a_t and substituting of $k_a = (\beta_t/\alpha_t)$ and $r_m^*/\alpha_t = \beta_t$

$$\frac{dx_t^*}{dt} = \beta_t \cdot \left[\frac{I}{\alpha_t} \cdot (x_f - x_t^*) - \frac{x_t^*}{\kappa_t + x_t^*} \right] \tag{65}$$

$$\frac{dx_f}{dt} = k_i \cdot I^{0.5} \cdot x_f + k_r \cdot (1 - x_f) \tag{66}$$

where

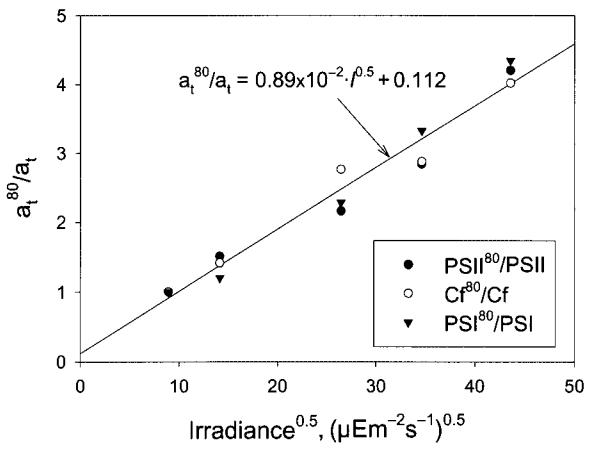

Figure 14. Variation in concentrations of various components (a_t) of the PSU with change in irradiance: Photosystems I (*PSI*) and II (*PSII*), cytochrome (*Cf*). The exponent 80 denotes the concentration value at 80 $\mu E \cdot m^{-2}s^{-1}$.

$$x_t^* = x^* \cdot x_f \tag{67}$$

and x^* represents the activated fraction of the functional PSUs. The dimensionless productivity is then calculated with Eq. (18).

If the irradiance changes in a cyclic pattern, Eqs. (63) and (64) can be rewritten as follows:

$$\frac{dx_t^*}{d\tau} = \frac{\beta_t}{\nu} \cdot \left[\frac{I}{\alpha_t} \cdot (x_f - x_t^*) - \frac{x_t^*}{\kappa_t + x_t^*} \right] \tag{68}$$

$$\frac{dx_f}{d\tau} = \left(\frac{k_i}{\nu} \right) \cdot I^{0.5} \cdot x_f + \left(\frac{k_r}{\nu} \right) \cdot (1 - x_f) \tag{69}$$

where ν is the frequency of the cycle and τ is the scaled time ($\tau = t \cdot \nu$).

Equations (65) and (66) [or Eqs. (68) and (69)] need to be solved simultaneously for any change in continuous irradiance. Because irradiance is generally a nonlinear function of time, an analytical solution may not exist for these equations and a numerical solution may be necessary. However, if we assume that irradiance varies slowly (e.g., diurnal light regimen of low frequency, ν), the process represented by Eq. (65) [or Eq. (68)] is fast compared with the rate of change of the irradiance. Consequently, x_t^* is close to equilibrium with the instantaneous irradiance (i.e., $x_t^* = x_{te}^*$). Therefore, from Eq. (65) (or Eq. (68)) it follows that

$$0 = \left[\frac{I}{\alpha_t} (x_f - x_{te}^*) - \frac{x_{te}^*}{\kappa_t + x_{te}^*} \right] \tag{70}$$

which has the following solution:

$$x_{te}^* = \frac{1}{2} \left[\left(x_f - \kappa_t - \frac{\alpha_t}{I} \right) + \sqrt{\left(x_f - \kappa_t - \frac{\alpha_t}{I} \right)^2 + 4\, \kappa_t\, x_f} \right] \tag{71}$$

Because $\kappa_t = \kappa \cdot x_f$ and $\alpha = \alpha \cdot x_f$, Eq. (71) can be rewritten as follows:

$$\frac{x_{te}^*}{x_f} = x_e^* = \frac{1}{2} \left[\left(1 - \kappa - \frac{\alpha}{I} \right) + \sqrt{\left(1 - \kappa - \frac{\alpha}{I} \right)^2 + 4\, \kappa} \right] \tag{72}$$

which is equivalent to Eq. (17). The fractional productivity is now calculated using Eq. (20), modified as follows:

$$\frac{P}{P_m} = \frac{I}{\alpha} (1 - x_e^*)\, x_f = \frac{I}{\alpha_t} x_f (1 - x_e^*)\, x_f = \frac{1}{\alpha_t} (1 - x_e^*) x_f^2 \tag{73}$$

Equation (73) includes the earlier noted relationship between α and α_t.

In summary, under slowly changing irradiance the integration of Eq. (66) (or Eq. (69)), provides x_f as a function of time. The instantaneous fractional productivity can be estimated using Eq. (73). The simulations presented illustrate how the dynamics of the model explain qualitatively and quantitatively the empirical observations such as the "afternoon depression" of photosynthesis by photoinhibition and the resulting hysteresis. These phenomena have been re-

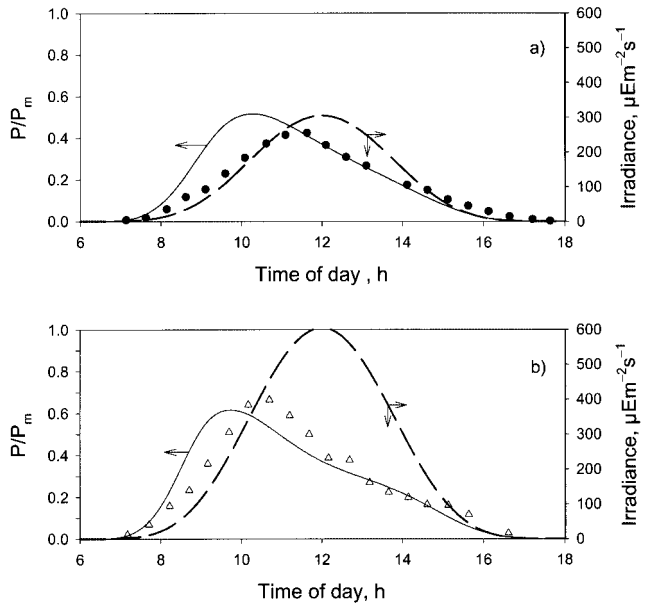

Figure 15. Diurnal variation in fractional productivity with time: (a) low peak irradiance; (b) high peak irradiance. The solid curves are model-derived. The irradiance profiles are shown by dashed lines.

ported commonly (Denman and Marra, 1986; Harris and Lott, 1973; Marra, 1978) under diurnally varying light regime. The mentioned studies showed from short-term measurements of oxygen evolution that the 'instantaneous' rate of photosynthesis on a *P-I* plot for a full day did not trace out a single *P-I* curve when the noon peak irradiance value was high. Hysteresis was observed as an adaptive response: A closed curve was produced with high rates in the morning, a midday depression, and recovery in the afternoon. However, the recovery was incomplete and the photosynthesis rate was lower in the afternoon than at the same irradiance in the morning. The extent of the hysteresis varied with the season (or the maximum irradiance in laboratory cultures) and with the extent of cloud cover over the previous few days.

Figure 15 shows the fractional productivity reported by Marra (1978) in optically thin and agitated cultures for diurnal cycles of low (Fig. 15a) and high (Fig. 15b) peak irradiance. The irradiance–time profiles and the model-predicted fractional productivity are also shown in Figure 15. In both cases, the shapes and the magnitudes of the model-predicted profiles are fairly consistent with the experimental data. Figure 15b (at higher peak irradiance than Fig. 15a), of course depicts the well-known photoinhibition which the model also simulates.

CONCLUDING REMARKS

The dynamic model of photosynthesis developed in this work accounts for photoadaptation, photoinhibition and the well-known "flashing light effect." The model explains photosynthesis–irradiance relationships observed typically for: (1) constant low irradiance; (2) constant intense irradiance; (3) flashing light; and (4) the diurnal irradiance cycle. In view of the model's ability to explain much of the independently published data, a square-root dependence of photosynthesis on irradiance seems justified. Similarly, Michaelis-Menten-type kinetics of consumption of the stored photochemical energy better explain the results than the assumptions used in the past.

This model is relatively easy to apply, because the photoadaptation and photoinhibition have been taken into account independently and with different time constants. For a fixed-illumination level the fraction of the activated PSUs reaches its steady-state value within seconds while the fraction of the functional PSUs reaches its steady-state value in hours. If a given level of illumination is maintained over days, the concentration of PSUs per cell reaches its optimal value.

NOMENCLATURE

ATP	Adenosine triphosphate
A*	Activated PSU
A^o	Nonactive or resting-state PSU
a	Total concentration of PSUs (no photoinhibition) (mol · cell^{-1})
a_f	Concentration of functional PSUs (mol · cell^{-1})
a_{nf}	Concentration of nonfunctional PSUs (mol · cell^{-1})
a_t	Total concentration of PSUs in photoinhibited culture (mol · cell^{-1})
80_t	Total concentration of PSUs at irradiance of 80 μE · m^{-2}s^{-1} (mol · cell^{-1})
a^*	Concentration of activated PSUs (mol · cell^{-1})
a^oC	Concentration of nonactivated PSUs (mol · cell^{-1})
a_e^*	Constant steady-state concentration of activated PSUs (mol · cell^{-1})
Cf	Cytochrome
Cf^{80}	Cytochrome concentration measured at 80 μE · m^{-2}s^{-1} (mol · cell^{-1})
$h\nu$	Photon
I	Irradiance (E · m^{-2}s^{-1})
I_c	Continuous irradiance (E · m^{-2}s^{-1})
I_m	Mean irradiance (E · m^{-2}s^{-1})
K_s^*	Constant in Eq. (5) (mol · cell^{-1})
k_a	Absorption coefficient (m^2 · mol^{-1})
k_c	Rate constant in Eq. (62) (s^{-1})
k_i	Rate constant in Eq. (7) (μE$^{-0.5}$m · s$^{-0.5}$)
k_P	Constant in Eq. (18) (–)
k_r	Rate constant of the recovery process (s^{-1})
NADHP	Nicotinamide adenine dinucleotide phosphate (reduced form)
P	Rate of photosynthesis (mol · cell^{-1}s^{-1})
$P(I)$	Rate of photosynthesis at irradiance I (mol · cell^{-1}s^{-1})
P-I	Photosynthesis-irradiance curve
P_m	Maximum rate of photosynthesis (mol · cell^{-1}s^{-1})
PSU	Photosynthesis unit
PSU_f	Functional PSU
PSU_{nf}	Nonfunctional PSU
PSU^o	Resting PSU
*PSU**	Activated PSU
PSI	Concentration of photosystem I (mol · cell^{-1})
PSI^{80}	Concentration of photosystem I at irradiance of 80 μE · m^{-2}s^{-1} (mol · cell^{-1})
PSII	Concentration of photosystem II (mol · cell^{-1})
$PSII^{80}$	Concentration of photosystem II at irradiance of 80 μE · m^{-2}s^{-1} (mol · cell^{-1})
r_m^*	Maximum rate of energy consumption (mol · cell^{-1}s^{-1})

r_1 Rate of photon capture step, given by Eq. (4) (mol · cell^{-1}s^{-1})
r_2 Rate of consumption of photochemical energy, given by Eq. (5) (mol · cell^{-1}s^{-1})
t Time (s)
t_c Characteristic time of the light/dark cycle; duration of light/dark cycle (s)
t_d Length of the dark period within one light/dark cycle (s)
t_f Duration of illumination (s)
x^* Fraction of functional activated PSUs (–)
x_e^* Steady-estate fraction of functional activated PSUs under continuous illumination (–)
x_f Fraction of functional PSUs (–)
x_{max}^* Maximum value of x^* under light-dark cycling (–)
x_{min}^* Minimum value of x^* under light-dark cycling (–)
x_t^* Fraction of activated PSUs (–)
x_{te}^* Steady-estate fraction of activated PSUs under continuous illumination (–)
x_1^* Root of Eq. (17) (–)
x_2^* Root of Eq. (17) (–)

Greek letters

α Parameter defined by Eq. (15) (E · m^{-2}s^{-1})
α_t Parameter equal to $\alpha \cdot x_t$ (E · m^{-2}s^{-1})
β Characteristic frequency (s^{-1})
β_t Parameter equal to r_m^* / a_t (s^{-1})
Γ Integration function defined by Eq. (53) (–)
δ Parameter in Eq. (24) (μE$^{-0.5}$m · s$^{-0.5}$)
ε Parameter defined by Eq. (55) (–)
κ Parameter defined by Eq. (15) (–)
κ_t Parameter equal to $\kappa \cdot x_t$ (–)
μ Specific growth rate (s^{-1})
ν Frequency of the light/dark cycle (s^{-1})
τ Dimensionless time ($= t \cdot \nu$) (–)
ϕ Dimensionless time defined by Eq. (30) (–)

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